



VIEWPOINT

Comparing Episodic, Chronic, Fishing, and Non-fishing Impacts on Resource Populations

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Since man uses the sea for transportation, waste disposal, and food, one goal of coastal management is to diminish the effect of the first two uses on the third. Doing so requires some appreciation of how episodic events such as from shipping accidents or dredging, and chronic stresses such as contamination from waste disposal, compare with fishing in terms of their impacts on living marine resources. These are all different stresses on individual fish and the issue resolves to extrapolating these stresses to the population level. It is not possible to quantify population effects precisely but it is possible to show that population effects of episodes and of chronic contamination can be compared with the effect of fishing.

Numerous authors have demonstrated the use of Leslie matrices to project population effects of different stresses (e.g. Vaughan and Saila, 1976; DeAngelis *et al.*, 1980; O'Neill *et al.*, 1981; Vaughan, 1981; Vaughan *et al.*, 1984; Schaaf *et al.*, 1987; Schaaf *et al.*, 1993). This paper is an expansion of Schaaf *et al.* (1987, 1993) with fishing explicitly included as one of the possible chronic impacts on population. A Leslie matrix is a matrix containing age-specific survival probabilities P_i and fecundities f_i . Where P_i is the probability of an individual surviving from year $t - 1$ to t and f_i is the fecundity (number of eggs per female) for fish of age t . With these parameters and relative numbers of individuals in each age-class in year t , multiplying the age-structure matrix by the survival and fecundity (the Leslie) matrix yields the age structure in year $t + 1$.

With an invariant matrix (i.e. the P 's and f 's remain the same for all years) all one is really doing is projecting populations by this formula:

$$S(t+x) = S(t) \exp(rx),$$

Age structure Year t	×	Survival & fecundity matrix	=	Age structure Year $t + 1$
N_0		$P_1 f_1$ $P_2 f_2$ $P_3 f_3$ $P_4 f_4 \dots P_n f_n$		N_0
N_1		P_1 0 0 0 \dots 0		N_1
N_2	×	0 P_2 0 0 \dots 0		N_2
N_3		0 0 P_3 0 \dots 0		N_3
N_4		0 0 0 $P_4 \dots$ 0		N_4
\vdots		\vdots \vdots \vdots \vdots \ddots		\vdots
N_{n-1}		0 0 0 0 \dots $P_{n-1} P_n$		N_{n-1}

where S is population size, r is the growth rate of the population and x is the number of years you wish to project. The equivalence of this in a Leslie matrix is that

$$r = \ln(\lambda),$$

where λ is the dominant eigenvalue of the matrix.

It is obvious that if $\ln(\lambda) > 0$ the population, given enough time, will become infinite. Similarly if $\ln(\lambda) < 0$ the population will become extinct. The population can only be stable if $\ln(\lambda) = 0$. Vaughan and Saila (1976) have derived a formula to adjust P_1 of a Leslie matrix so that $\lambda = 1$. It is recognized that, in reality, population sizes of feral animals vary greatly from year to year but that over the long term there is a stable age distribution around which the annual fluctuations occur. Adjusting P_1 to stabilize the matrix simply allows comparisons among various simulated effects on the P 's and f 's. It is the ability to manipulate the individual elements of the matrix that makes it so attractive a way to simulate and compare among different ways of affecting populations.

Figs. 1–4 are results of using this model to project croaker (*Micropogonias undulatus*) population over 50 years given various impact scenarios. The life-history data (i.e. the P 's and f 's) for that population are reported (Schaaf *et al.*, 1987) to be $P = 0.27$ for all years except

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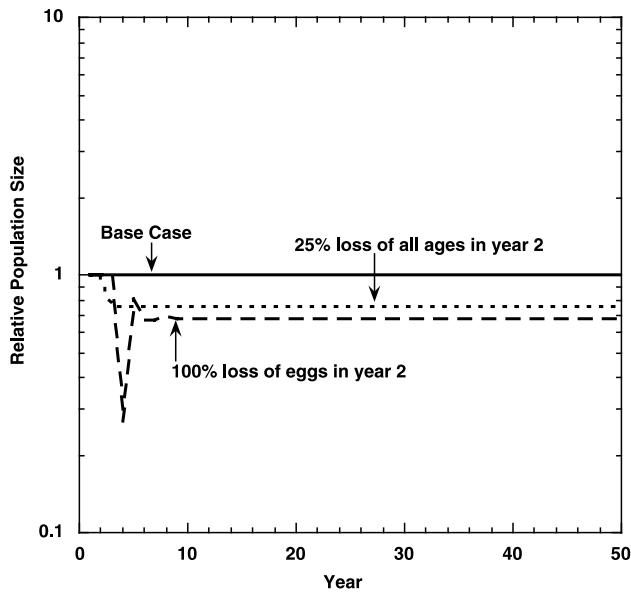


Fig. 1 50-year population projection for base case (steady state) and with single-year catastrophes that eliminate all eggs or 25% of all age-classes.

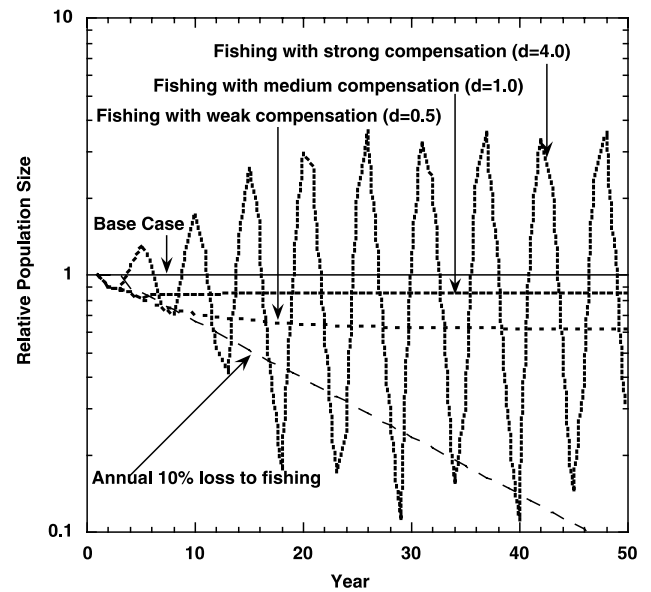


Fig. 3 50-year population projections for annual (i.e. chronic) 10% additional fishing mortality with weak, medium, or strong density-dependent compensation.

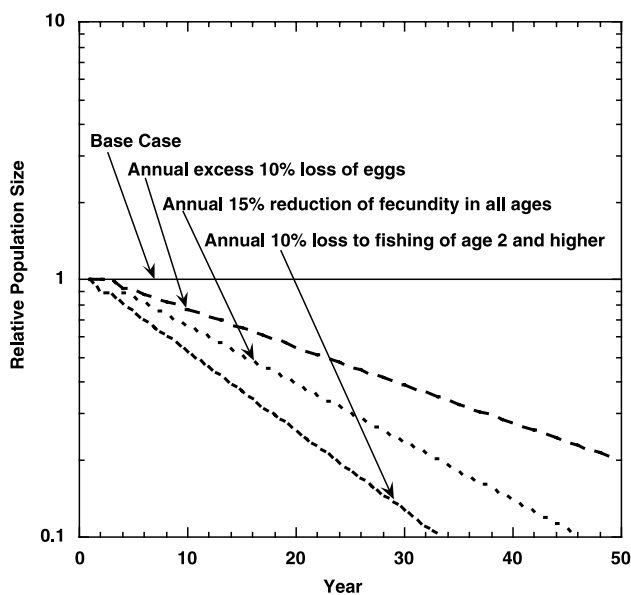


Fig. 2 50-year population projections for annual (i.e. chronic) 10% excess (beyond steady state) loss of eggs, 15% decreased fecundity of all ages, 10% additional fishing mortality.

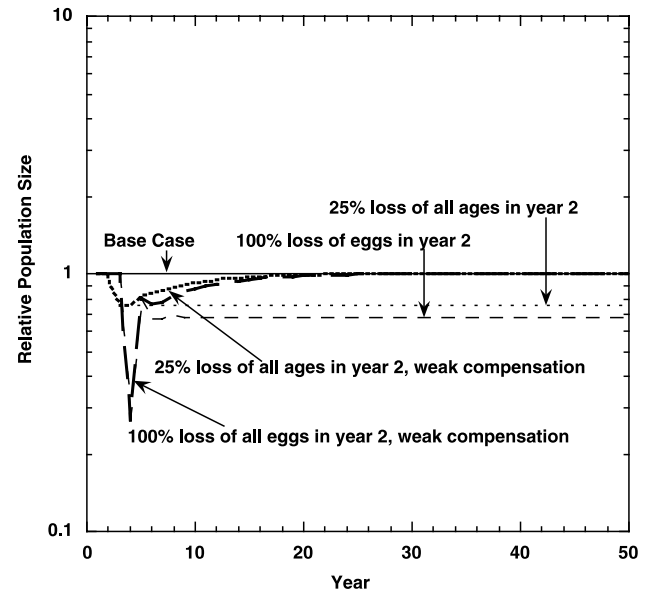


Fig. 4 50-year population projections for single-year catastrophes and weak density-dependent compensation.

P_1 , $f = 118, 385, 682, 1111, 1841, 2483$, and 3267 (all times 1000) eggs per females of age 1–7, respectively. The calculated P_1 required for steady state is 1.2×10^{-5} (i.e. one egg in 83000 becomes a one-year-old fish). These data provide a concrete example but fundamental comparisons among various impacts illustrated in the figures are independent of any particular set of life history data or simulated extents of impact. In all figures, population changes are plotted relative to the base case in terms of numbers of 2+ -year-old fish. If the resource for a particular species consists of younger (or only older) fish, the basic comparisons remain unchanged.

Fig. 1 shows three cases: (1) the base case (no impacts) with P_1 set to its steady-state value, and the cases where, in a single year, no eggs become one-year-old fish, (2) and (3) where survival is decreased by 25% for all eggs and all fish of all ages. If no eggs survive in one year, the population rebounds in subsequent years but never reaches its original steady-state value. If all ages suffer reduced survival in one year, the entire population decreases to a lowered level for all subsequent years. In both cases with one catastrophic year, P_1 is at its steady-state value in all except that one year, so $\lambda = 1$ in all but that year, and the population returns to steady, but lower, level.

Fig. 2 compares the base case with three chronic impacts: (1) a 10% permanent decrease in N_0 as could occur with eggs or larvae exposed to contamination, (2) a 20% permanent decrease in all the f 's as could occur with adults suffering reproductive damage because of exposure to contamination, and (3) a 10% permanent decrease in the P 's for all two-year-old and older fish as could occur with increased fishing effort. All of these impacts set the population on a permanent downward track. The first just decreases N_0 every year and the others force λ to be always < 1 . Permanently decreasing N_0 by a given percentage and decreasing all the f 's by the same percentage would be mathematically identical and constitute identical impacts. For a given percent reduction, increased fishing always has the larger population effect than impacts on the zero-year-class or on fecundity because fishing removes individuals from all except the youngest age-classes and all the eggs those fish would have contributed.

Fig. 3 repeats Fig. 2 (for fishing) but with three levels of density-dependent compensation that increase P_1 as N_0 decreases according to

$$P_1 = P_{1,\text{steady}} \exp(d(1 - N_0)/N_{0,\text{steady}}),$$

where $P_{1,\text{steady}}$ and $N_{0,\text{steady}}$ are the P_1 and N_0 under the base condition, and $d = 0.5, 1$, or 4 all of which are arbitrary but progressively stronger density-dependencies.

Fig. 3 demonstrates the importance of feedback in maintaining populations in the face of excess mortality. In this particular case the feedback is assumed to occur through increased success of eggs in the presence of fewer eggs but there are other possibilities such as increased fecundity or survival of adults. The exact mechanism is unimportant but the principle is essential. In the absence of density-dependent compensation, the projections in Fig. 2 would apply showing that chronic excess mortality would eventually drive populations to extinction. Since fishing is excess mortality but is nonetheless a sustainable exploitation of marine resources, density-dependent compensation must exist. Stocks can be overfished and driven almost to extinction when exploited to an extent that overwhelms compensation but the fact that there is an acceptable level of exploitation argues for the existence of compensation. The only possible exception would be complete stochasticity whereby the size of a year-class is unrelated to any prior year making any deterministic model irrelevant. It would then be impossible to conclude that impacts on fish in any year would have long term population consequences. Versions of Fig. 3 could be presented like Fig. 2 where, instead of fishing, the excess mortality occurs via losses of annual eggs and larvae or losses of fecundity. Such plots would be identical to Fig. 3 in showing in that compensatory mechanisms would prevent an inexorable drive to extinction.

Recognizing that density-dependent compensation exists is not the same as quantifying it. The three dif-

ferent strengths used in Fig. 3 are arbitrary. The highest one only demonstrates that if the assumed feedback is very strong, the resulting relationship can approach chaos (May, 1976) and is unrealistic. Nonetheless, while it is not quantifiable, feedback exists. Fig. 4 repeats the single-year catastrophes of Fig. 1 but with the weak density-dependence applied to Fig. 3. Here, the important point is that the same feedback that allows fishing to be a viable enterprise also greatly diminishes the effect of very bad years. In fact, it erases the effect of catastrophes over a time period determined by life history parameters of the population and the strength of density-dependent compensation.

There are many ways to simulate randomness and a figure could be included to acknowledge that just random noise applied to P_1 in the base case (no impacts on any year-classes and no density-dependence) produces population projections that cover the ranges induced by the various impacts with and without density-dependence. Even with detailed knowledge of the annual mortality imposed by cooling water intakes on white perch (*Morone americana*), Vaughan and Van Winkle (1982) concluded that random noise in year-class sizes would prevent detection of an annual loss of even 50% with less than 20 years of field data. Given the known interannual variability in year-class sizes of Atlantic menhaden (*Brevoortia tyrannus*), Vaughan *et al.* (1986) concluded that single catastrophic years that decrease an entire year-class by less than 70% (or the entire fished population of 2+-year-olds by less than 40%) would not be detected in annual catch statistics.

There are much more subtle uses of a Leslie matrix than exemplified here where it has been forced to represent only the stationary condition (invariant age distribution). This is the condition asymptotically approached by populations as arbitrary initial age distributions proceed with constant survival and fecundity values. Caswell (1989) has demonstrated the power of matrix algebra in exploring the non-stationary as well as stationary conditions and sensitivity of populations individual elements of the matrix. Fox and Guervitch (2000) building on the analytical groundwork of Caswell for non-stationary cases have demonstrated the dependence of matrix elements and therefore population projections on the actual numbers of individuals in each age group.

Such extensions of the basic matrix can be mathematically complex but do not alter the basic points that (1) different types of impacts whether episodic or chronic can be compared on the common basis of how they would affect future populations, (2) density-dependent compensation must either exist or future population sizes are independent of past impacts, (3) density-dependent compensation eventually erases the population effects of single-year catastrophes and (4) fishing has a more severe effect on future populations than chronic impacts that decrease only first-year survival or fecundity. Moreover, the 10% and 15% con-

tinuous non-fishing impacts simulated in Fig. 2 are rather large and would have to be imposed over wide spatial scales to actually occur. These points need to be kept in mind to put non-fishing impacts in the context of fishing effects on resource populations.

Rather than inserting more graphical examples into this paper, an executable program (LeslieGAME.exe and source code) is available from the author and on the internet (<ftp://spo.nos.noaa.gov/public/Lesfile>) which illustrates all its points by allowing the reader to simulate different levels and types of impacts and different levels of density dependence with 25 sets of life history data (including those for croaker) taken from DeAngelis *et al.* (1980), O'Neill *et al.* (1981), Vaughan (1981), and Schaaf *et al.* (1987). The author recognizes this to be a simple application of a Leslie matrix and that much more sophisticated applications are commercially available.

Views expressed here are those of the author and not necessarily those of the National Oceanic and Atmospheric Administration.

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